

## A Fair Deal for the Devonian Arthropoda Fauna of Rhynie

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Though the original authors of the Rhynie fauna took the Devonian age of it for granted, later authors considered part of the fauna to be contaminants. There is no intrinsic proof for such a statement. Recently, several specimens of *Rhyniella praecursor* Hirst & Maulik 1926 were found to be embedded in the same, single phase of mineralisation of the siliceous, which applies to the Devonian flora. The assumption of contamination has led to a Thysanoptera from Rhynie remaining undescribed for at least 15 years and for a non-appreciation of the Pterygota in the Devonian.

### 1 General remarks on the Rhynie chert

It is a common event in science that certain discoveries are ill-fated. This may result from the work of a gifted investigator who lived too early; in other words: a work towers over its contemporaries and is not understood; the new statement goes unheeded.

The same is true if an independent mind states a clear case, but authorities deride it: Mendel contra Naegeli, Fuhlrott contra Virchow, Robert Mayer contra Helmholtz and Poggendorf. Another case is more complicated: a multiparameter undertaking is more liable to come to naught than a single parameter undertaking. Columbus was convinced his whole life, that he had reached India by the W' route. Or for instance the fauna from the Devonian silicified peat bog of Rhynie: this is a border case. The effort is palaeobotanical, the fauna, as a by-product, is palaeozoological.

As a fossil record of small terrestrial Devonian Arthropoda does not exist nor one from the Lower Carboniferous, the appreciation of the Rhynie fauna is not only exposed to misconception; the appreciation is conditioned by the current opinions on Arthropoda evolution and on evolution in general. On the other hand, the siliceous matrix of the Rhynie Chert is not absolutely unique as a fossilizing medium of smaller Arthropoda, but so rare, that no author of the Rhynie fauna could easily provide himself with suitable examples from other localities. For the authors of the Rhynie fauna no comparison with another occurrence of Micro-Arthropoda offered itself, the fauna of the different fossiliferous resins being an example, but no biostratonomic recourses to this material were made. Rhynie provides evidence for 3 orders of the Arachnida, 1 of the Crustacea, and probably 3 of the Insecta (Fig 1).

Representatives of the Arachnida, Crustacea and Insecta are to be found in the nodule fauna from the English Midlands and from Mazon Creek in Illinois of Upper Carbonifer-

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ous age [Rolfe 1980]. However the specimens are considerably larger than those at Rhynie.

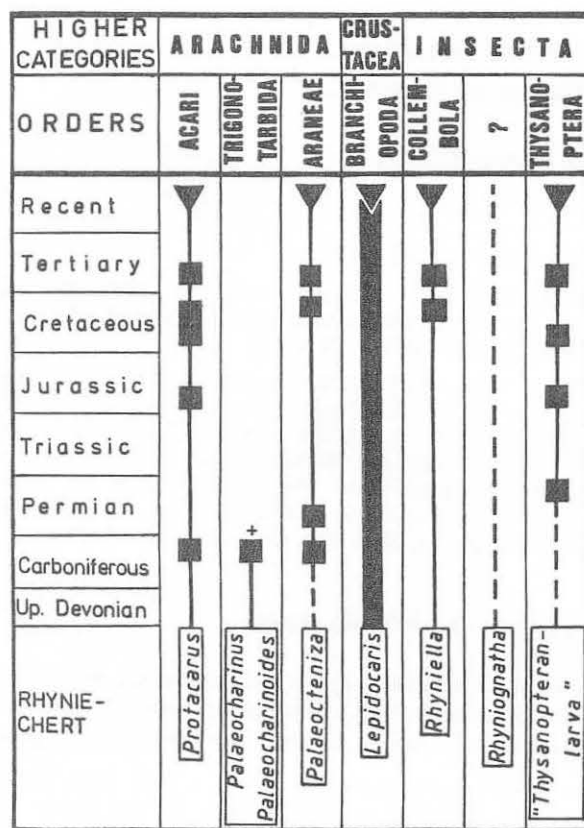


Fig 1: Stratigraphic record of the higher categories and orders of Arthropoda which are supported by different Genera from the Lower Devonian Rhynie Chert, Scotland. Wide beams give a more or less continuous fossil record for each order, thin lines indicate fossil gaps but presumable connections, interrupted lines show doubtful relations.

## 2 Palaeozoological occurrences and their interpretations by different authors

Hirst [1923], Hirst & Maulick [1926], Scourfield [1926 and 1940] and Tillyard [1928] described the Rhynie fauna. The first faunal paper by Hirst is published 5 years later than the first palaeobotanical paper on Rhynie by Kidston & Lang [1917].

In none of the original papers on the fauna appears a doubt about the genuine Devonian age of the faunal components. But the preservation, apart from shrinkage, from the accidents of biostratonomy and from the preparation, is so perfect at Rhynie that the idea of recent animals actually having crept in, has suggested itself to some authors over the last decades. For instance, doubts about the Devonian origin of part of the Rhynie fauna are to be found in a statement of R. A. Crowson [1970: 65-66]:

"The well-known palaeobotanist, Professor J. Walton, some years ago showed me a rock-

section of Rhynie Chert containing what he thought to be an insect. After some study, I was able to recognize it as a nymphal thysanopteran, representing quite an advanced group of winged insects. It seemed fairly evident to me that the insect was a modern contaminant of the rock specimen."

Kevan et al [1975] made reference to the presumable Ectognatha *Rhyniognatha hirsti* Tillyard 1928 (Fig 1, 2f):

"The mandibles are reminiscent of the sharp bladed and toothed jaws of a carnivore. Tillyard (1931) hints that they may be thysanuran and Hirst and Maulick suggest they may be larval. The former suggestion does not seem probable and the latter is unlikely as it would require the existence of holometabolous insects in the Devonian."

W.D.J. Rolfe in Panchen refers to some of the Rhynie taxa [1980: 127]:

"It is worth recording that Crowson came to this view [i.e. the mite *Protacarus crani* Hirst (1923) being a contaminant] as a result of a section of Rhynie Chert referred to him by the late John Walton. It contained a thysanopteran insect nymph which Crowson was able to identify with a living form, that must have crawled into a crevice in the chert."

There is an obvious contradiction between Crowson's and Rolfe's statements: Crowson recognized a nymphal form of a Thysanoptera representing quite an advanced group of winged insects. Rolfe stated the section "contained a thysanopteran insect nymph which Crowson was able to identify with a living form ...". It is clear that Crowson did not intend to say that the Rhynie Thysanoptera was a living form.

Whalley & Jarzembowski [1981] however, describing part of the Collembola *Rhyniella praecursor* Hirst & Maulik 1926 (Fig 1 and 2e, under consideration of the new morphological features) with intact abdomen, state after a mineralogical examination not performed by themselves that the chert containing the insect is homogeneous with the surrounding rock and represents a single phase of mineral growth. Whalley & Jarzembowski continue: "We conclude that *Rhyniella praecursor* is of Lower Devonian age (possibly Siegenian)."

### 3 Conclusion: Are the macrocomponents of Devonian age, the microcomponents a cenozoic contamination?

You will gather from the citation of the first 3 authors that not one of them states reasons for his doubts. It is hence permitted to say: in order to negate the Devonian age of some Rhynie taxa — the mite *Protacarus*, the Collembola *Rhyniella* and the undescribed and unnamed possible Thysanoptera nymph — one has been content to assume a contamination with cenozoic or even subrecent crevice-seekers. Nobody took the trouble to give the contentious specimens to a mineralogist, so that he may judge on the secondary mineralisation of healed cracks, in which the contaminating taxa had found shelter, as did Whalley & Jarzembowski [1981].

The "doubts" confront us with 2 different components of Macro- and Micro-Arthropoda at Rhynie. The freshwater inhabiting Crustacea *Lepidocaris* sp, the Trigonotarvida *Palaeocharinus* sp, which can be as large as 14 mm and *Palaeocharinoides* sp (Fig 2b) suggest a Devonian age. The stratigraphic record of the presumable Araneae *Palaeoecteniza* sp (Fig 2c) has not been discussed, nor that of *Rhyniognatha hirsti*, the ectognath pair of mandibulae (Fig 1f). An additional Arthropoda, *Heterocrania rhyniensis* has also been described but is too fragmentary to be interpreted as a Chelicerata. *Protacarus*, the many specimens (at least 12) of the Collembola *Rhyniella* and the possible Thysanoptera nymph are said to be cenozoic or subrecent contaminants. Nobody, however, has pointed

to a difference in colour, tracht, preservation or any other biostratonomically limiting factor of the one faunal component, compared with the other. By dividing the Rhynie fauna into 2 components of different origin and history, the authors deride earlier biostratonomic and paleological implications, performed mutually and in a reciprocal action both by Palaeobotanists and Palaeozoologists. The authors take the "two components fauna"-theory into account, to avoid at all costs the acceptance of three remarkable taxa as Devonian in age. Such practice defies the principle of parsimony, the principle of Occams razor.

For more than 15 years a pterygote from the Lower Devonian has been determined as a Thysanoptera nymph. Instead of being hailed as the oldest Pterygota representative known of it is mentioned twice as a curiosity "which must have crawled into a crevice in the chert" [Rolfe 1980], or, which "I was able to recognize as a nymphal Thysano-

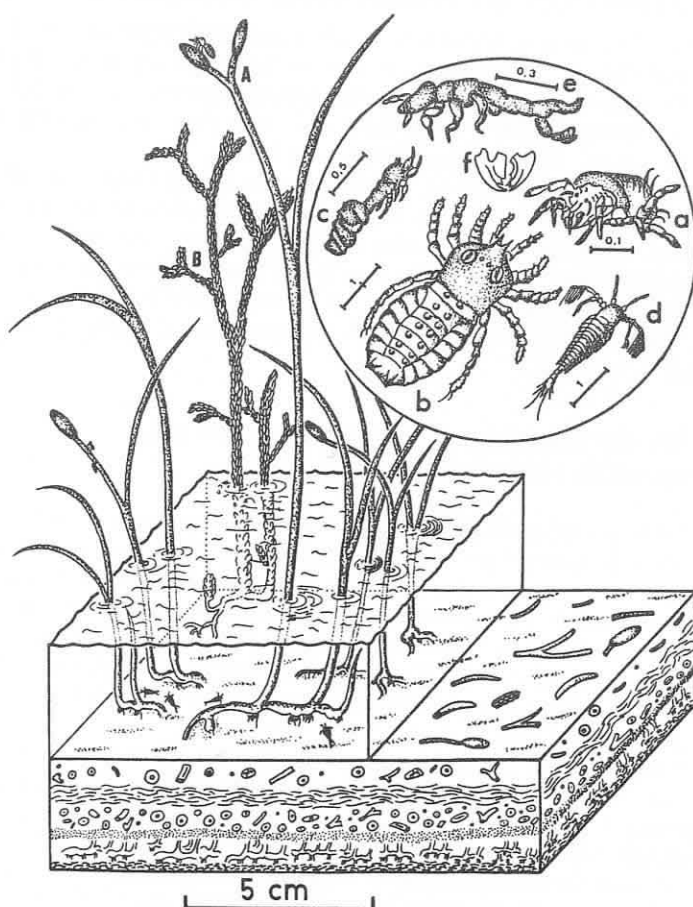


Fig 2: Reconstruction of a semiaquatic to terrestrial Palaeobiocenosis in the Lower Devonian of Rhynie, Scotland. — 2A *Rhynia major* Kidston & Lang 1917; 2B *Asteroxylon mackiei* Kidston & Lang 1917; 2a *Protacarus crani* Hirst 1923; 2b *Palaeocharinus* sp.; 2c *Palaeoeteniza crassipes* Hirst 1923; 2d *Lepidocaris rhyniensis* Scourfield 1926; 2e *Rhyniella praecursor* Hirst & Maulick 1926; 2f *Rhyniognatha hirsti* Tillyard 1928.

pteran, ... (and) ... it seemed fairly evident to me that the insect was a modern contaminant of the rock specimen" [Crowson 1970]. The other Pterygota from the Devonian, – *Eopteron devonicum* Rohdendorf 1961, from the Upper Devonian of Timan – is meanwhile recognized as the Uropodita of an Eumalacostraca (Crustacea).

But the evidence of Thysanoptera in the Devonian really means something unexpected, just as the fossil mammal *Amphitherium* Author 0000 from the British Middle Jurassic (Bathonian) was unexpected for some scientists in the early 19th century. But what do palaeontologists find in general? The unexpected! And they are continually forced to revise their previous statements about the fossil record of any taxon, because the record improves. A recent discovery may predate a taxon by an unexpected 200 million years. The Upper Carboniferous lamprey from the Mazon Creek of Illinois is separated by  $\pm 300$  million years from its recent relatives; no other fossil lamprey bridges the gap in the fossil record. The same is true for many higher categories of the Arachnida, for most freshwater Crustacea. But we have been programmed to accept their authenticity because the relevant fossils have been found in concretions of proven origin and in a condition where "contamination" or faking is out of the question.

#### 4 The palaeobiocenosis as a unit

If we accept the Devonian Thysanoptera, we have to accept the existence of the sister-groups of the Thysanoptera in the Devonian, ie almost all other subgroups of the Ectognatha, except for the Holometabola. Consequently we have also to consider in Rhynie a highly advanced semiaquatic (fresh water) to terrestrial ecosystem, in which already complicated interrelations between producers (plants), primary consumers (herbivores) and carnivores and predators existed (Fig 2). Wootton [1972] states that the successful evolution of the earliest insects started in the role of small predators, feeding predominantly on primary consumers, because here they had only few competitors in other groups. Later insects "developed the morphological and behavioural equipment to exploit a wider range of food-sources and came to comprise a great variety of macro- and micro-feeders operating at all levels, from within the substrate to the top of the surface film." [Wootton 1972: 79]. Although the author of this article also neglected the palaeobiocenosis of the Rhynie Chert for the reconstruction of early freshwater to terrestrial ecosystems, his theoretical scenario has been adopted and shows parallels to the palaeontological facts, of course necessarily including both macro- and micro-components in such a fauna.

The acceptance of the Rhynie Thysanoptera as Devonian in age would promote the search for kindred fossils all over the world. If on any past occasion the whole faunal list of Rhynie had been published with measurements and with the number of specimens, the contamination blunder would have been smothered before it began. An investigation on the apparent absence of a Micro-Arthropoda fauna from the Carbiniferous Coalball Flora, seems to be a profitable undertaking which is overdue.

#### 5 Acknowledgements

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